ANATOMY OF KOEBERLINIA AND CANOTIA REVISITED

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ABSTRACT

Detailed anatomical descriptions of leaves and stems are presented for *Koeberlinia* and *Canotia,* desert perennials of North America with photosynthetic old stems. *Koeberlinia* has linear subulate leaves with conical unicellular trichomes, adaxial stomata, abundant palisade mesophyll, and relatively few tannin cells; whereas *Canotia* has deltoid scales lacking trichomes and having abaxial stomata, undifferentiated mesophyll, and abundant tannin cells. Stem anatomy of these genera is also dissimilar even though both have adaptations to facilitate stem photosynthesis. Myrosin cells are present in inner cortex of *Koeberlinia.* Woods are superficially similar in vessel and fiber dimensions; however, *Canotia* has low, narrow rays with abundant resin and prismatic crystals, whereas *Koeberlinia* has higher, wider rays lacking resin and crystals, and its vessels appear to have vestured pits. Bark anatomy of these genera is fundamentally different. A previous report of secretory ducts in *Koeberlinia* is incorrect. Those features shared are judged to be convergent, and the differences are great enough to negate their classification together in the bigeneric Koeberliniaceae. A recommendation is made to reassign *Canotia* to Celastraceae and *Koeberlinia* to or near Capparaceae.

Koeberlinia and *Canotia* are xeromorphic, nonsucculent perennials of North America that have spine-tipped, aphyllous, photosynthetic old stems. Whereas Metcalfe and Chalk (1950), Benson (1957), Takhtajan (1969, 1973), and Hutchinson (1973) classify these desert plants in the bigeneric family Koeberliniaceae, most recent treatments place *Koeberlinia* in Capparoideae of Capparaceae (Melchior, 1964; Airy-Shaw, 1966, 1973; Cronquist, 1968; Thorne, 1968, 1976; Novák, 1972), separating *Canotia* from *Koeberlinia* for reassignment, presumably in or near Celastraceae. Johnston (1975) lists the known similarities between *Acanthothamnus* (Celastraceae), which also has old green stems, and *Canotia,* supporting inclusion of *Canotia* in that family. Only Metcalfe and Chalk make anatomical comparisons of *Koeberlinia* and *Canotia,* these based on scanty material and Record's (1926) wood diagnosis of *Koeberlinia* that lacks illustrations; they do not cite Record's (1938) wood description of *Canotia* and previous descriptions of *Koeberlinia* stem anatomy (Cannon, 1908; Pax and Hoffman, 1936). Moreover, Airy-Shaw (1966, 1973) has questioned their report of resin ducts in *Koeberlinia.* This study expands descriptions of and more fully illustrates vegetative anatomy of *Koeberlinia* and *Canotia* so that their relationships may be reviewed.

METHODS

Samples of *Koeberlinia spinosa* Zucc. from three disjunct populations in Cochise County, Arizona (*Gibson 3243, 3263, 3463*), *Canotia holacantha* Torr. from northern Arizona (*Burgess 5481*; *Gibson 3154*),

MADROÑO, Vol. 26, No. 1, pp. 1–52, June 20, 1979

and *C. wendtii* M. C. Johnst. from Chihuahua, Mexico (*Burgess 5212*) were collected and preserved in formalin-acetic acid-alcohol fixative (Johansen, 1940). Herbarium vouchers are in ARIZ. Additional wood microslides of *Koeberlinia* from California (*Gill 451, 453*: POM), provided by Dr. Sherwin Carlquist, and the original microslide of Record (1926; *Yw 8959*), loaned by the Forest Products Laboratory, Madison, were examined for wood descriptions.

Wood and bark sections were cut on a sliding microtome at 20 μm and stained with safranin. Wood macerations were prepared using Jeffrey's method (Johansen, 1940) and also stained with safranin. Measurements were made with an optical micrometer on sections except those on cell length, which were obtained from macerations. Means of cell dimensions were based on 25 measurements for each sample. Vessel pitting was observed at 1000× using an Eastman Kodak No. 11 green filter.

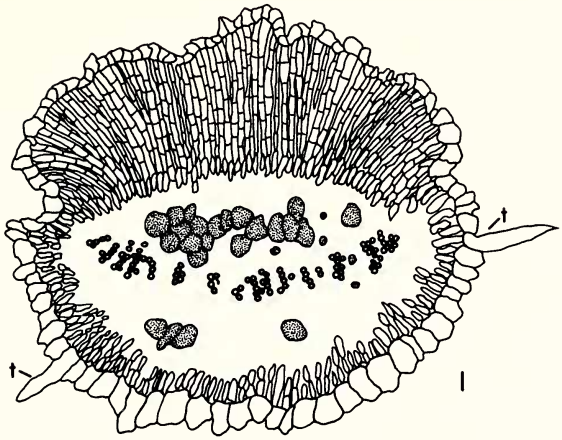
Stems and leaves were embedded in paraffin, sectioned at 10 or 15 μm, and stained with safranin and fast green. All drawings were prepared by tracing photomicrographs.

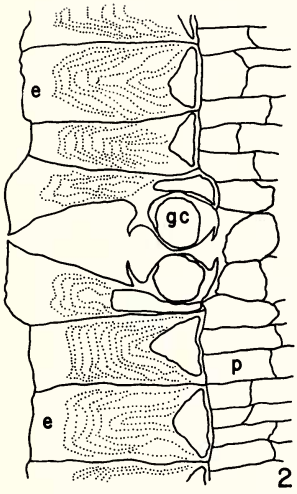
Anatomical Descriptions

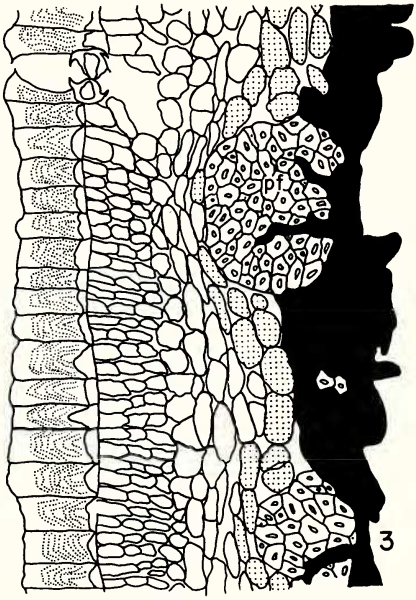
Koeberlinia

Leaves. Leaves linear-subulate, somewhat curved, 1.5–2.2 mm long, caducous, present only on very young vegetative shoots. Epidermis (Fig. 1) uniseriate; cells with markedly convex outer walls. Stomata sunken in depressions; epistomatic. Trichomes unicellular, conical with rounded tips, to 100 μm long, scattered over leaf surface. Lamina absent. Palisade chlorenchyma highly developed on adaxial side, much less so on abaxial side. Tannin cells in undifferentiated mesophyll. Primary xylem conspicuous and abundant, forming wide arc across leaf.

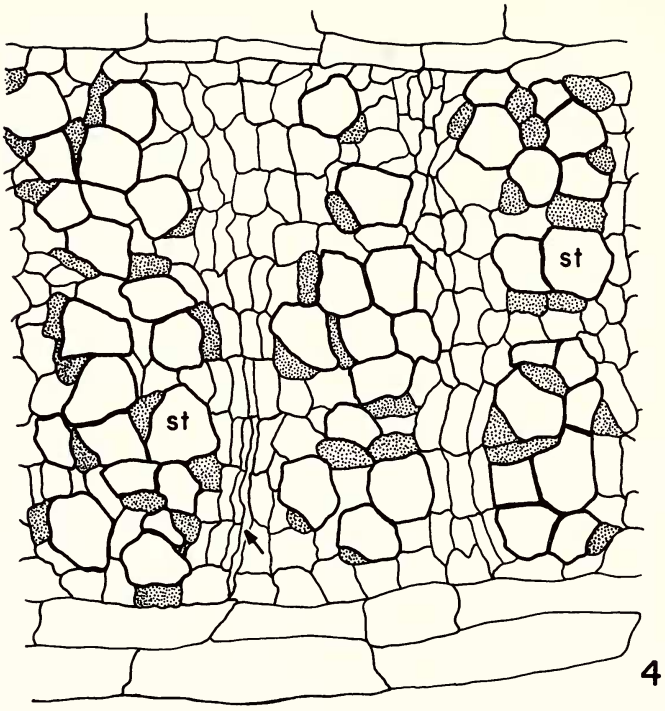
Green stems. Stems bright green, evenly tapering to a sharp point. Epidermis (Figs. 2, 3) uniseriate, soon becoming radially elongate with onset of secondary growth, which is precocious; outer walls excessively thickened with concentric layers of wall material (not radial as illustrated in Pax and Hoffman, 1936), impregnated with cuticle. Trichomes frequent; unicellular and conical with rounded tips; walls thickened like epidermis. Stomata anomocytic; sunken in pits when groundmass epidermis increases in length; outer and small inner ledges present. Chlorenchyma to 0.2 mm thick, palisade cells not markedly elongate. Inner cortex with *spheroidal idioblastic myrosin cells*. Sclerenchyma beneath chlorenchyma, beginning as small groups of primary phloem fibers, later forming a closed ring by differentiation of brachysclereids from parenchyma. Primary phloem with small rounded solitary crystals. Secondary phloem (Figs. 4, 5) with bands of sieve tubes and companion cells in alternation with several layers of paren-







FIGS. 1–3. *Koeberlinia spinosa*. 1. Leaf transection, showing epidermis with trichomes (t), palisade of mesophyll, tannin cells (heavy stipple) in undifferentiated ground tissue, and a wide arc of primary xylem vessels (small circles). ×100. 2. Green stem transection; outer secondary walls of epidermis (e) develop eccentrically with concentric layering, overarching stomatal guard cells (gc) with prominent ledges. Palisade (p) of cortex is not well developed. ×350. 3. Green stem transection; beneath photosynthetic tissues are myrosin cells (light stipple) and clusters of phloem fibers (pf) interconnected by brachysclereids (black), which differentiate relatively late in stem development. ×190.



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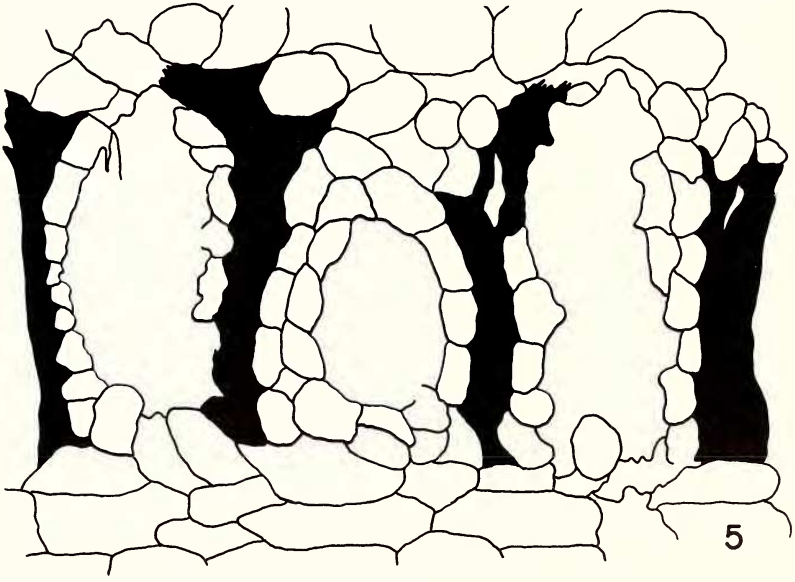

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chyma having thin walls. Sieve tube walls fairly thick; fibers absent. In outer secondary phloem, parenchyma cells enlarged and separate, forming large spaces in tissue; old bands of sieve tubes and companion cells compressed into thick, irregular band of cell wall material (Fig. 5); these spaces the "secretory (resin) canals" of Metcalfe and Chalk (1950; dried phloem also splits along these bands of parenchyma). Pith with lignified secondary walls shortly following the start of secondary growth; often with abundant prismatic to rounded solitary crystals.

Stem wood. Sapwood yellowish white, sharply defined; heartwood dense, chocolate brown. Growth rings present, usually sharply defined; wood ring-porous (Fig. 6). Pores distributed evenly throughout each growth layer; 150–175 mm^{-2} of transection. Pores circular or oval in outline. Pore diameter medium-sized to moderately small in earlywood (24–212 μm; means 43–149 μm) to very small and extremely small in latewood (means 20–49 μm). Pores mostly solitary, rarely in twos. Maximum vessel wall thickness 8 μm found in widest pores, decreasing to 1.5 μm in narrowest pores. Vessel-element length medium-sized to extremely short (68–384 μm; means 198–310 μm), longest in largest stems. Perforation plates exclusively simple; end walls nearly transverse to diagonal; tails sometimes present, especially in latewood elements. Lateral walls of vessels with numerous rows of alternate, bordered pits, 5–6 μm across; *pits inconspicuously vestured* (Fig. 8; needs SEM verification) pit aperture nearly horizontal and linear. Tertiary helical thickenings usually present. Tyloses absent but gum deposits present in some pores of heartwood. Tracheids enucleate, nonseptate, very short (means 425–588 μm), and extremely small (13–27 μm). Maximum fiber wall thickness 7.5 μm; pits abundant and conspicuous, pit diameter 4–6 μm; tertiary helical thickenings present but inconspicuous. Axial parenchyma usually abundant, apotracheal diffuse or diffuse-in-bands and scanty paratracheal; accumulating dark substance in heartwood. Rays (Figs. 6, 7) mostly multiseriate, usually 4–7 cells wide, but some biseriate and uniseriate, height 70–1200 μm; 7–9 mm^{-1}. Rays homogeneous, cells long-procumbent, lacking crystals except in very young stems where ray cells of innermost xylem have occasional solitary crystals resembling those of pith; dark substance present but not abundant in rays of heartwood, as in axial parenchyma. Storying absent.

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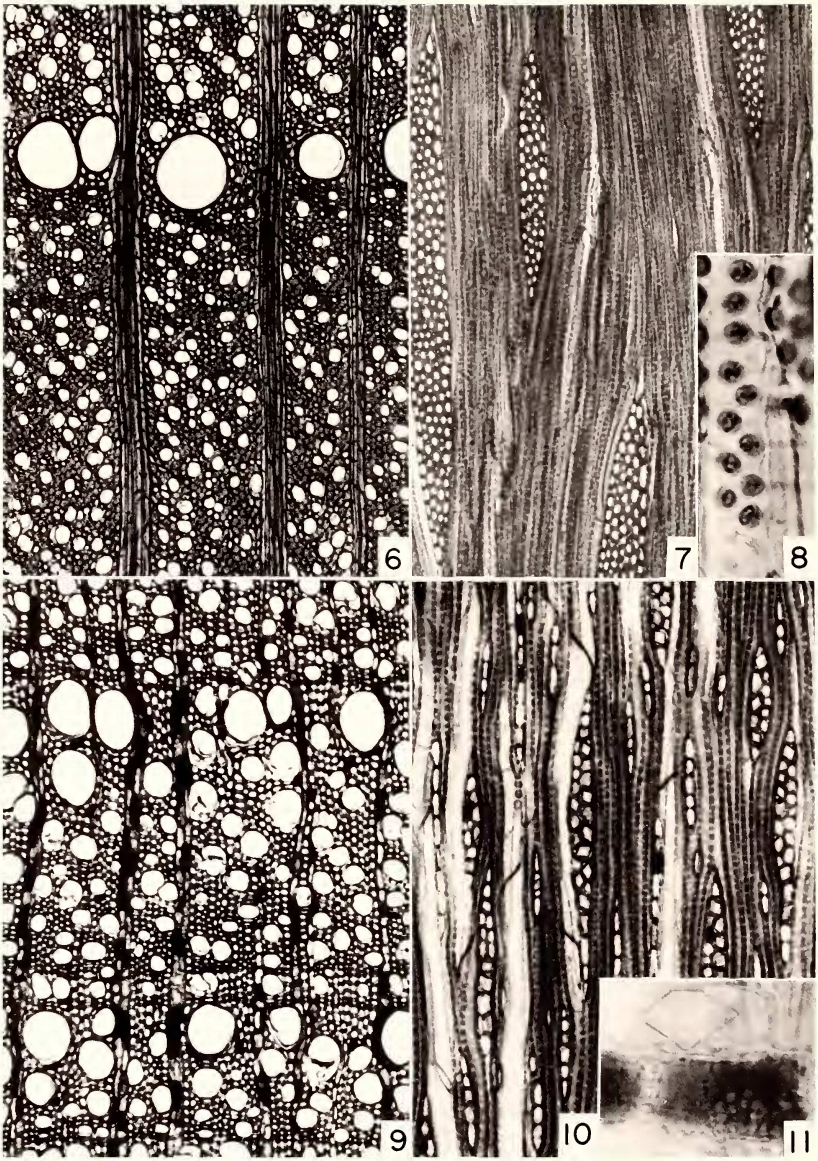
FIGS. 4–5. *Koeberlinia spinosa,* secondary phloem transections. ×500. 4. Inner conducting region composed of sieve tubes (st) having thickened walls, companion cells (heavy stipple), and parenchyma. Arrow indicates where parenchyma between growth layers has begun to split. 5. Outer region where sieve tubes and companion cells are crushed (black) and periclinal splits have developed in bands of parenchyma, resembling resin ducts but nonsecretory.



FIGS. 6–11. 6–8: *Koeberlinia spinosa,* wood. 6. Transection, showing ring porosity. ×110. 7. Tangential section. ×110. 8. Tangential section; vessel with vestured bordered pits on lateral walls. ×700. 9–11: *Canotia holacantha,* wood. 9. Transection; ring-porous wood in which vessels are abundant; dark staining cells in the narrow rays contain resin. ×110. 10. Tangential section, showing numerous low uniseriate and biseriate vascular rays often containing resin cells. ×110. 11. Radial section of same at high magnification, where resin- and crystal-bearing cells of the ray are observed. ×750.

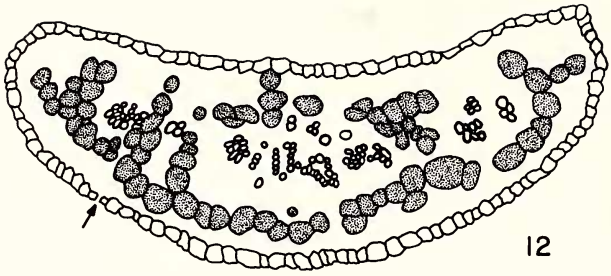
Root wood, Gibson 3243. Similar to stem wood of the stem plant except as follows: growth rings less distinct; vessel-element length and diameter slightly greater; and tracheid length greater (mean 624 μm).

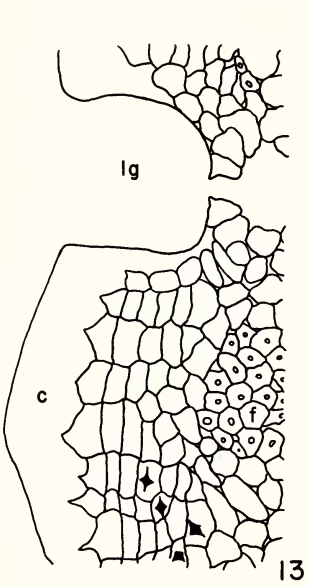
Canotia

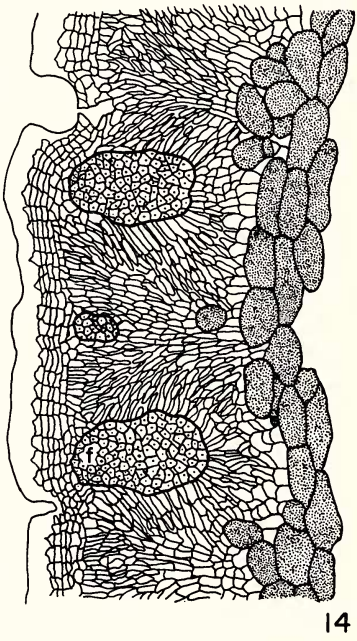
Leaves. Leaves minute caducous deltoid scales, 1–2 mm long. Epidermis (Fig. 12) uniseriate; outer wall somewhat thickened. Stomata sunken slightly; hypostomatic. Trichomes absent although multicellular glandular trichomes abundant in leaf axil, these with tannins. Lamina absent. Mesophyll undifferentiated, no palisade cells, but many interior cells having abundant tannins. Vascular tissue forming a wide arc across leaf.

Green stems. Stems pale green, to more than 1 cm diam. Epidermis (Figs. 13, 14) uniseriate at first, then dividing periclinally, even before the onset of secondary growth, to produce a multiple epidermis with 4 or more cells in a radial file; innermost cells often with solitary rhomboidal crystals; outer walls impregnated with and covered by cutin, to 45 μm thick. Trichomes as above. Stomata sunken in deep longitudinal grooves when multiple epidermis forms; outer and inner ledges present. Chlorenchyma about 250 μm thick in mature stems, palisade cells highly developed. Subepidermal clusters of thick-walled unlignified cortical fibers with minute lumina (gelatinous in *C. wendtii*), precocious in origin. Innermost chlorenchyma with solitary rhomboidal crystals. Ring of tangentially ovoid, large tannin cells beneath chlorenchyma. Primary phloem (pericyclic?) fibers present but delayed in development; thick walled. Secondary phloem axial system with broad bands of sieve tubes and parenchyma interrupted by groups or bands of bast fibers. Pith sclerified early; tannins cells very abundant; crystals uncommon.

Stem wood. Sapwood yellowish; heartwood fairly dense, somewhat purplish-brown. Growth rings of sapwood fairly distinct with the naked eye; semi-ring to ring porous (Fig. 9). Pores distributed evenly and abundant throughout each growth layer; up to 200 mm^{-2} of transection. Pores tending to be radially ovoid in earlywood and irregular in outline in latewood. Pore diameter moderately small in earlywood (23–113 μm; means 53–73 μm) to extremely small in last-formed latewood (means 22–28 μm), gradually decreasing from earlywood to latewood; mean earlywood pore diameter widest in widest growth layers, increasing also from inner to outer wood. Pores almost exclusively solitary, rarely in twos. Maximum vessel wall thickness 3 μm found in widest pores, decreasing to 1 μm in narrowest pores. Vessel-element length medium-sized to extremely short (138–723 μm; means 234–447 μm). Perforation plates exclusively simple; end walls nearly transverse (widest elements) to diagonal with long tails (narrowest elements). Lateral walls of vessels with numerous rows of alternate, bordered pits, to 6 μm across; pits not vestured; pit aperture







FIGS. 12–14. *Canotia holacantha*. 12. Leaf transection, showing epdiermis with abaxial stomate (arrow), tannin cells in undifferentiated ground tissue (heavy stipple), and a wide arc of primary xylem vessels (small circles). ×150. 13. Green stem transection; longitudinal grooves (lg) are formed by periclinal divisions of protoderm, producing a multiple epidermis that is heavily cutinized (c). Some parenchyma cells contain prismatic crystals (dark bodies); clusters of fibers (f) occur opposite multiple epidermis. ×350. 14. Green stem transection; beneath multiple epidermis palisade cells are well developed, even radiating from clusters of fibers (f). Primary phloem is enclosed by a ring of tannin cells (heavy stipple). ×100.

nearly horizontal and linear. Tertiary helical thickenings present and conspicuous in vessels. Tyloses absent. Tracheids enucleate, nonseptate, very short (means 432–825 μm), and extremely small (to 20 μm). Maximum fiber wall thickness 4.5 μm; pits abundant and conspicuous, pit diameter to 6 μm, often wider than on vessels; pit aperture diagonal; tertiary helical thickenings present but inconspicuous. Axial parenchyma apotracheal diffuse and occasionally diffuse-in-bands and scanty paratracheal; heartwood axial parenchyma usually containing abundant resin. Rays (Figs. 10, 11) uniseriate and biseriate, rarely triseriate; height 25–620 μm; up to 20 mm^{-1}. Ray heterocellular, cells mostly square to slightly procumbent; containing abundant resin in heartwood and inner sapwood, and solitary prismatic crystals throughout (Fig. 11); integumented. Storying absent.

Root wood, Burgess 5481. Similar to stem wood of the same plant except as follows: growth rings less distinct; pore diameter slightly greater because larger in earlywood and latewood; and tracheid length shorter.

Discussion

Metcalfe and Chalk (1950) correctly noted that *Koeberlinia* and *Canotia* show similar young stem structure, but the factual sources for their comparisons are not apparent; an anatomical description of *Koeberlinia* is compared with an illustration of *C. holacantha,* the structure of which is not discussed. When compared closely, one observes many differences between the two genera. *Koeberlinia* has stem vesture, a single-layered epidermis with stomata sunken in individual pits, poor development of cortical palisade, idioblastic myrosin cells in cortex, an ensheathing ring of pericyclic sclerenchyma, and no tannin cells. *Canotia* has no trichomes except in leaf axils, a multiple epidermis with stomata sunken in longitudinal grooves, prominent bundles of cortical fibers, strong development of cortical palisade, no myrosin cells, and an ensheathing ring of tannin cells. Moreover, the nature and distribution patterns of crystals in the two genera are fundamentally different. Features shared, e.g., thick cuticle, sunken stomata with ledges, and fairly wide chlorenchyma, are similarities expected from plants in which photosynthesis by old, leafless stems is the chief source of carbon assimilation for the plant, i.e., adaptations related to penetration of light, plant water status, and gaseous exchange. In fact, outer stem features of these species more closely resemble other unrelated aphyllous perennials with spine-tipped green stems than each other (Gibson, unpubl. data).

Although leaves of *Koeberlinia* and *Canotia* are ephemeral, vestigial organs, their structural designs are quite dissimilar. Their similarities include only the great amount of vascular tissues and tannins present. Both leaves resemble a midvein in structure and could have

arisen convergently by a loss of marginal meristems, which are usually responsible for blade formation.

The account of Metcalfe and Chalk (1950) incorrectly characterized phloem of *Koeberlinia* as having secretory canals. These authors observed young stems from dried herbarium material and, consequently, probably observed artifactual splitting in phloem growth layers along zones of weakness in parenchyma. In bark, this splitting occurs naturally as tissues are stretched to accommodate increases in stem circumference. This splitting superficially looks like resin ducts because the openings appear to be lined with epithelium. Secondary phloem of *Koeberlinia* and *Canotia* differs significantly, especially in the banding patterns of axial elements and the abundance in *Canotia* of bast fibers, which are absent in *Koeberlinia*.

Woods of *Koeberlinia* and *Canotia* are superficially very similar in that their vessel elements and tracheids are closely comparable in dimensions and wall features, and the three species have ring-porous woods (to semi-ring-porous in *Canotia*). Nonetheless, these woods are different on the basis of the vessel pits and rays; *Koeberlinia* has vestured pits on vessels and relatively wide vascular rays whereas *Canotia* lacks vestured pits and has very numerous, low, narrow rays with abundant resin- and crystal-bearing cells. Prismatic crystals are generally absent in woods of *Koeberlinia*. Moreover, *Koeberlinia* tends to have more conspicuous and numerous axial wood parenchyma.

Woods of nonsucculent perennials from arid and semi-arid habitats typically have numerous, very short, narrow vessel elements with simple perforation plates, multiseriate alternate lateral-wall pitting, and, in many cases, tertiary helical thickenings, and the vessels characteristically occur in large groups (Webber, 1936; Carlquist, 1966, 1975, 1977). Woods of *Canotia* and *Koeberlinia* are noticeably xeromorphic except that vessel grouping is completely lacking. For desert plants, wood similarities have arisen convergently so many times that citing similarities between dimensions and wall features of axial elements from two xeromorphic taxa is unwarranted for drawing systematic conclusions.

Johnston (1975) clearly rejected the classification of *Canotia* and *Koeberlinia* in the same family, a proposal dating from Engler (1895) and Barnhart (1910), and he noted how *Canotia* fits comfortably in Celastraceae near *Acanthothamnus*. *Acanthothamnus* is unknown anatomically, so comparisons cannot be made. Nevertheless, Record (1938) concluded that woods of *Canotia* are quite typical for Celastraceae.

Given that *Koeberlinia* must be reclassified apart from *Canotia,* one must look first to Capparaceae, into which most authors have classified *Koeberlinia* on reproductive features. This anatomical study sheds new light on that placement. Species of Capparaceae, as well

as Brassicaceae, have vestured pits on vessels and myrosin cells, features individually uncommon in angiosperms as a whole and quite unusual occurring together. All aspects of *Koeberlinia* stem anatomy also fit within the range of features recorded in woody Capparaceae (Metcalfe and Chalk, 1950), including crystal and sclerenchyma patterns. Therefore, assignment of *Koeberlinia* to Capparaceae is justifiable, and the significant remaining problem is to determine to which capparaceous genus *Koeberlinia* is most closely related. I expect the closest extant relative to possess normal secondary xylem, myrosin cells, and xeromorphic tendencies as well as similar design of reproductive features such as pollen (Martin and Drew, 1969). When these comparisons are completed, recognition of the monotypic Koeberliniaceae (Kearney and Peebles, 1960; Shreve and Wiggins, 1964; Correll and Johnston, 1970; Munz, 1974) will undoubtedly be judged unwarranted.

ACKNOWLEDGMENTS

I thank those who provided material for this study. I am indebted to Dr. Regis Miller, Forest Products Laboratory, Madison, who provided technical help on wood diagnoses and suggested a search for vestured pits.

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(Accepted 26 Dec 1978.)